

## Functional Osteology of the Primate Carpus With Special Reference to Strepsirhini

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**KEY WORDS:** wrist morphology; positional behavior; lemuriforms; postcranial evolution

**ABSTRACT** Preuschoft et al. ([1993] in H. Preuschoft and D. Chivers (eds.): *Hands of Primates*. New York: Springer-Verlag, pp. 245–256) used a theoretical biomechanical analysis to generate several predictions relating subordinal differences in primate hand proportions to differences in carpal morphology. This study tests these predictions using quantitative analyses of carpal morphology between extant haplorhine and strepsirhine primates. Results show that living strepsirhines have a significantly larger hamate hamulus than do haplorhines, supporting Preuschoft et al.'s (1993) predictions. Extant strepsirhines also have a significantly shorter pisiform body than do haplorhines and arboreal nonprimate eutherians and a larger scaphoid tubercle than New and Old World monkeys. These results contrast markedly with those expected under Preuschoft et al.'s (1993) model. Furthermore, strepsirhines and haplorhines do not differ significantly in the relative size of their radiocarpal articulations. These morphometric observations do not match the predicted morphological patterns because the kinematic assumptions upon which the biomechanical models are based are incorrect. Living strepsirhines appear to be derived in having very deep radial and ulnar margins of the carpal tunnel for well-developed extrinsic digital flexors. Moreover, tooth-combed prosimians differ from most haplorhines, early Tertiary adapiforms, and arboreal nonprimate eutherians in having a relatively short pisiform body, which gives the flexor carpi ulnaris less power to flex the wrist from extended (= dorsiflexed) positions. These structural observations suggest that powerful manual grasping and an emphasis on leaping and climbing, rather than palmigrade quadrupedal walking and running, are morphotypic for extant Strepsirhini. *Am J Phys Anthropol* 104:105–116, 1997. © 1997 Wiley-Liss, Inc.

A general survey of hand morphology across the Order Primates reveals a tremendous degree of variation in relation to different postural, locomotor, and manipulatory behaviors (e.g., Midlo, 1934; LeGros Clark, 1959; Bishop, 1964; Etter, 1974; Jouffroy et al., 1991; Hamrick, 1996a,b; Hamrick and Alexander, 1996). Primate hand proportions are in particular quite variable, with many strepsirhines such as lorises having an elongate fourth digit, a condition known as ectaxony (Jouffroy et al., 1991). In contrast,

the third digit is the longest ray of the hand in many haplorhine primates such as tarsiers and humans, a condition referred to as mesaxony (Jouffroy et al., 1991).

Preuschoft et al. (1993) defined some stereotyped primate hand postures which they

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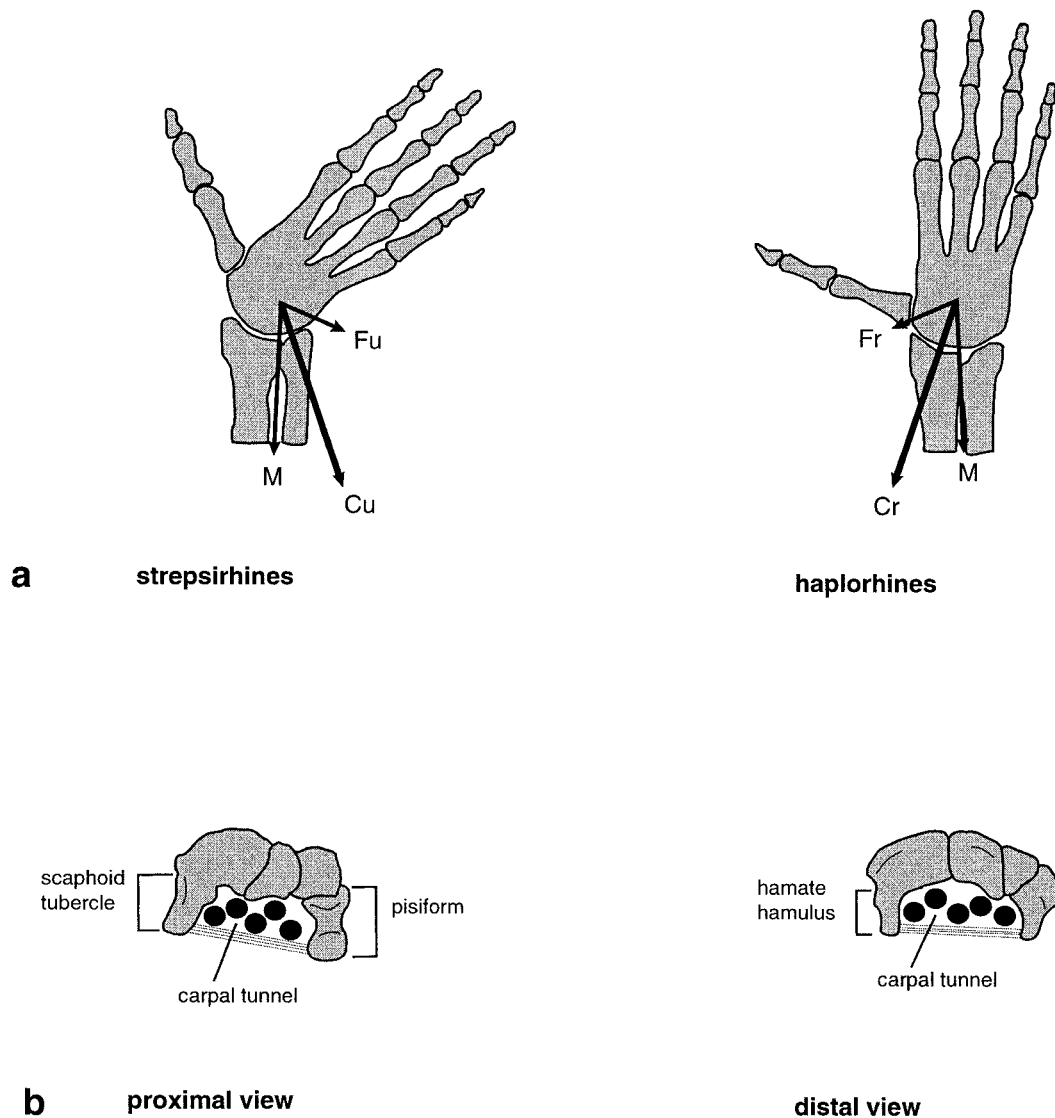


Fig. 1. **a:** Ectaxonic hand of strepsirhines and mesaxonic hand of haplorhines showing the more ulnarly deviated hand of strepsirhines. The resultant muscle force (Cu) from the digital flexors (M) has a large component (Fu) directed towards the ulnar margin of the wrist in strepsirhines. In contrast, the resultant force (Cr) from the flexors (M) has a large component (Fr) directed towards the radial margin of the wrist in haplorhines. **b:** The ulnar borders of the carpal tunnel (e.g., the pisiform body and hamate hamulus) and the

ulnocarpal articular surfaces are therefore expected to be relatively expanded in strepsirhines in order to stabilize the carpus during contraction of the digital flexors. The radial border of the carpal tunnel (e.g., the scaphoid tubercle) and the radiocarpal articular surfaces are expected to be relatively expanded in haplorhines in order to stabilize the carpus during contraction of the digital flexors. Modified and redrawn from Preuschoft et al. (1993).

believed characterized “the ectaxonic hand of most strepsirhines and the mesaxonic [hand] of many, especially ground-dwelling, monkeys, apes, and humans” (Preuschoft et al., 1993, p. 245). Their analysis of strepsi-

rhine hand biomechanics was based upon the following assumptions: 1) the grasp is a pincer grasp between digit I and the post-axial rays and 2) the hand is ulnarly deviated on arboreal supports (Fig. 1). In con-

trast, their analysis of haplorhine hand biomechanics assumed that 1) the digits are placed in line with the long axis of the support and 2) the hand is not significantly ulnarly deviated (Fig. 1).

Preuschoft et al.'s (1993) model predicts that the strepsirhine carpus should experience an ulnarly directed resultant muscle force produced by contraction of the long digital flexors during manual grasping (Fig. 1). Strepsirhines should therefore have relatively large ulnocarpal articular surfaces and ulnar borders of the carpal tunnel in order to reduce stress on the bones and joints produced by this resultant force. In contrast, haplorhine carpals should experience a radially directed resultant muscle force produced by the long flexors (Fig. 1). Thus, haplorhines are expected to possess expanded radial articular elements and radial borders of the carpal tunnel.

The purpose of this study is to test the morphological predictions germane to these biomechanical models in order to elucidate some similarities and contrasts in carpal morphology between strepsirhine and haplorhine primates. These morphologies are then analyzed from a functional perspective in order to reconstruct the pattern of carpal form and function morphotypic for the primate Suborder Strepsirhini. Finally, these data on carpal form and function are used as a basis for inferring the locomotor and postural behaviors present in the last common ancestor of tooth-combed primates.

## MATERIALS AND METHODS

### Sample

Subordinal differences in carpal morphology were examined in an extant skeletal sample of 34 haplorhine and strepsirhine primate species of which 33 are different genera (Table 1). Over 350 individuals were included in this sample, composed of approximately 90 haplorhines and over 250 strepsirhines. The haplorhines range in body size from approximately 130 g in the case of *Tarsius* up to 20 kg in *Papio anubis*, whereas the strepsirhines range in size from approximately 215 g in *Galago senegalensis* up to 10 kg in *Indri* (Fleagle, 1988). Several preserved specimens of each suborder were also dissected. This sample is designed to include

TABLE 1. Extant strepsirhine and haplorhine skeletal specimens included for analysis<sup>1</sup>

Haplorhines	Strepsirhines
<i>Tarsius</i> spp. <sup>2</sup> (7)	<i>Cheirogaleus major</i> <sup>3</sup> (8)
<i>Saguinus oedipus</i> <sup>2</sup> (6)	<i>Lemur fulvus</i> <sup>4</sup> (20)
<i>Saimiri sciureus</i> <sup>2</sup> (10)	<i>Lemur catta</i> <sup>4</sup> (19)
<i>Callithrix jacchus</i> <sup>2</sup> (6)	<i>Varecia variegata</i> <sup>3</sup> (19)
<i>Callimico goeldii</i> <sup>3</sup> (5)	<i>Hapalemur griseus</i> <sup>4</sup> (21)
<i>Aotus trivirgatus</i> <sup>3</sup> (5)	<i>Lepilemur mustelinus</i> <sup>4</sup> (24)
<i>Ateles paniscus</i> <sup>3</sup> (3)	<i>Indri indri</i> <sup>4</sup> (22)
<i>Alouatta palliata</i> <sup>2</sup> (4)	<i>Propithecus verreauxi</i> <sup>4</sup> (22)
<i>Pithecia pithecia</i> <sup>2</sup> (3)	<i>Avahi laniger</i> <sup>4</sup> (13)
<i>Miopithecus talapoin</i> <sup>2</sup> (5)	<i>Daubentonia madagascarensis</i> <sup>4</sup> (8)
<i>Macaca</i> spp. <sup>2</sup> (4)	<i>Otolemur crassicaudatus</i> <sup>4</sup> (19)
<i>Papio anubis</i> <sup>3</sup> (6)	<i>Galago senegalensis</i> <sup>4</sup> (7)
<i>Colobus guereza</i> <sup>3</sup> (3)	<i>Euoticus elegantulus</i> <sup>4</sup> (11)
<i>Presbytis frontatus</i> <sup>2</sup> (3)	<i>Loris tardigradus</i> <sup>4</sup> (8)
<i>Procolobus verus</i> <sup>2</sup> (3)	<i>Nycticebus coucang</i> <sup>4</sup> (20)
<i>Hylobates</i> spp. <sup>2</sup> (6)	<i>Arctocebus calabarensis</i> <sup>4</sup> (4)
	<i>Perodicticus potto</i> <sup>4</sup> (17)

<sup>1</sup> The number of individuals included for each species is shown in parentheses.

<sup>2</sup> Mesaxonic.

<sup>3</sup> Paraxonic.

<sup>4</sup> Ectaxonic.

both haplorhines and strepsirhines covering a similar range of body masses. The large-bodied hominoids were excluded from analysis primarily because there are no living strepsirhines of similar size that could be included for comparison.

The overwhelming majority of these haplorhines are mesaxonic—that is, the third ray is over 3% longer than the fourth ray. The strepsirhines are primarily ectaxonic, where the fourth ray is over 3% longer than the third ray. Paraxonic species are defined as those in which the third and fourth rays are similar in length to within 3% of one another. These distinctions (Table 1) are based on the hand proportion data set published by Jouffroy et al. (1991). Hand skeletons of one early Tertiary primate (*Notharctus tenebrosus*, AMNH 127167) (Hamrick and Alexander, 1996) and three nonprimate eutherian mammals, *Procyon* (Carnivora), *Sciurus* (Rodentia), and *Tupaia* (Scandentia), were also included to expand the comparative data set. These taxa are intended to represent outgroups useful for assessing the phylogenetic valence of some of the traits discussed in this paper.

### Osteometrics and statistical analysis

Linear dimensions of the carpal tunnel borders, such as dorsopalmar lengths of the

scaphoid tubercle (STL) and hamate hamulus (HAL), radioulnar diameters of the radiocarpal (RCW) and ulnocarpal (UCW) articular surfaces, and dorsopalmar height of the pisiform body (PISH), were taken with dial calipers (Fig. 1). Breadth of the radiocarpal articular surface (RCW) was measured as radioulnar diameter of the radiocarpal articular facet on the distal radius, whereas breadth of the ulnocarpal articular surface (UCW) was measured as radioulnar diameter of the ulnocarpal articular facet on the distal ulna. Previous workers (Swartz, 1989; Godfrey et al., 1991) have suggested that joint surface areas are preferable over linear diameters as estimates of joint size. In order to test whether or not radioulnar diameter of the radiocarpal articular surface is a reliable predictor of radiocarpal articular area, I regressed  $\log_{10}$  radiocarpal articular area (dependent variable) against  $\log_{10}$  radioulnar diameter of the radiocarpal articular surface (independent variable). Radiocarpal area was calculated from dorsopalmar and radioulnar arc lengths taken from epoxy-resin casts with a Reflex microscope (see Hamrick, 1996a,c) using the formula for the area of an ellipse ( $\pi \times 1/2 \text{dorsopalmar arc length} \times 1/2 \text{radioulnar arc length}$ ). Results indicate that, within a sample of 266 individuals from over 20 haplorhine and strepsirhine species, radiocarpal area is significantly correlated with radioulnar diameter of the radiocarpal facet ( $r = .99$ ,  $P < .001$ , slope = 1.88, y intercept =  $-.56$ , S.E.E. = .13), indicating that radiocarpal diameter is a reliable predictor of radiocarpal articular area.

Subordinal differences in primate carpal joint morphology were examined by performing several between-group statistical tests on pooled-sex mean species values. The body size estimate used as the independent variable in these bivariate analyses is the mean of humeral midshaft diameter and mediolateral diameter of the distal calcaneal articular facet. A regression between published mean species body weights and species means for the skeletal estimate used here demonstrate that this composite measure is both significantly correlated ( $r = .99$ ) and virtually isometric (slope = .34) with body size. Ordinary least-squares (OLS) analysis

TABLE 2. Summary of regression analyses for haplorhine and strepsirhine carpal dimensions against estimated body size<sup>1</sup>

Measurement	Y intercept	Slope	r
<b>Haplorhines</b>			
RCW	.24 (.23)	.98 (.99)	.99
UCW	-.19 (-.22)	.71 (.73)	.97
PISH	.41 (.37)	.83 (.85)	.98
STL	-.73 (-.83)	1.04 (1.09)	.95
HAL	-1.24 (-1.49)	1.05 (1.18)	.89
<b>Strepsirhines</b>			
RCW	.15 (.11)	1.04 (1.07)	.97
UCW	-.63 (-.81)	.99 (1.10)	.90
PISH	-.35 (-.49)	1.11 (1.19)	.93
STL	-.44 (-.56)	1.02 (1.09)	.93
HAL	-.53 (-.81)	.83 (1.0)	.82

<sup>1</sup> Ordinary least-squares values are shown above reduced major-axis values, which are in parentheses. Measurement abbreviations are explained in the text.

of covariance (ANCOVA) was used to test for subordinal differences in carpal joint dimensions relative to this body size estimate. Tsutakawa and Hewett's (1977) quick test was used as a second, nonparametric bivariate approach. The reduced major axis regression model (RMA) (Clarke, 1980) was chosen for this nonparametric test because neither the X nor Y variable was measured without error (Harvey and Pagel, 1991). Correlations between carpal dimensions and estimated body size are quite high in most cases, and results using each regression technique are very similar (Table 2). Subordinal differences in carpal joint shape were also explored using a multivariate discriminant function analysis performed on log-transformed variables. A multivariate analysis of variance (MANOVA) was the preferred technique for this analysis since the taxonomic groups were defined a priori (Neff and Marcus, 1980).

## RESULTS

Bivariate plots of radiocarpal and ulnocarpal diameters against estimated body size show considerable overlap between the two suborders in relative size of the carpal joint articular surfaces (Fig. 2). Strepsirhines tend

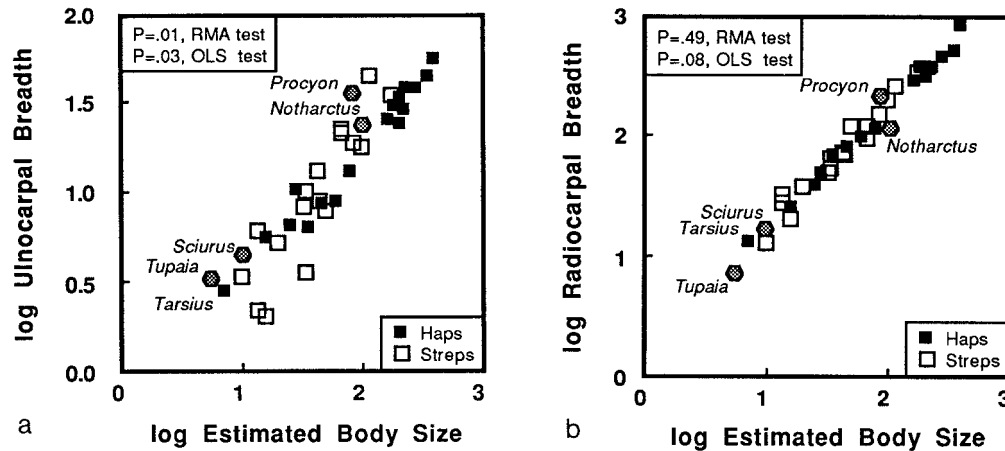


Fig. 2. Bivariate plots of (a) ulnocarpal and (b) radiocarpal breadth against estimated body size in strepsirhines (open squares) and haplorhines (closed squares). Fossil and nonprimate taxa (shaded) are labeled.

TABLE 3. ANCOVA tests (haplorhines vs. strepsirhines) for the carpal dimensions included for analysis<sup>1</sup>

Measurement	RMA quick test	OLS slope test	OLS y intercept test
RCW	ns	ns	ns
UCW	**	*	
	(strepsirhines > Y)	(strepsirhines > slope)	
PISH	**	**	
	(haplorhines > Y)	(strepsirhines > slope)	
STL	***	ns	***
	(strepsirhines > Y)		(strepsirhines > Y)
HAL	**	ns	**
	(strepsirhines > Y)		(strepsirhines > Y)

<sup>1</sup> Measurement abbreviations are explained in the text. ns,  $P > .05$ .

\*  $P < .05$ .

\*\*  $P < .01$ .

\*\*\*  $P < .001$ .

to have a higher slope for their ulnocarpal dimensions relative to body size (Table 2) and in fact differ significantly ( $P < .05$ ) from haplorhines in this respect (Table 3). Visual inspection of the bivariate scatter, however, reveals that there is considerable overlap between the two suborders within intermediate body size ranges (Fig. 2a). The smaller lorises, which are the most ectaxonic of all the primates (Jouffroy et al., 1991), have relatively reduced ulnocarpal diameters, whereas the paraxonic *Varecia* has a relatively expanded ulnocarpal joint (Fig. 2a). Thus, if there is any correlation between degree of ectaxony and relative size of the ulnocarpal joint, it would appear to be a negative correlation. Bivariate analyses (Table 3) and visual inspection of bivariate plots (Fig. 2b) show no differences between

strepsirhine and haplorhine primates in relative breadth of the radiocarpal articular surface.

The two suborders do, however, differ in morphology of the proximal carpal tunnel borders—that is, in relative size of the scaphoid tubercle and pisiform body. Tree shrews and monkeys tend to have a relatively short scaphoid tubercle, whereas the tubercle is more elongate in strepsirhines (Fig. 3a). *Notharctus* and *Tarsius*, like living strepsirhines, have a relatively elongate scaphoid tubercle, suggesting that this is likely a primitive primate trait (Fig. 4a). Bivariate tests show that strepsirhines differ significantly ( $P < .001$ ) from haplorhines in relative scaphoid tubercle length (Table 3), with strepsirhines having a relatively longer scaphoid tubercle than haplorhines across



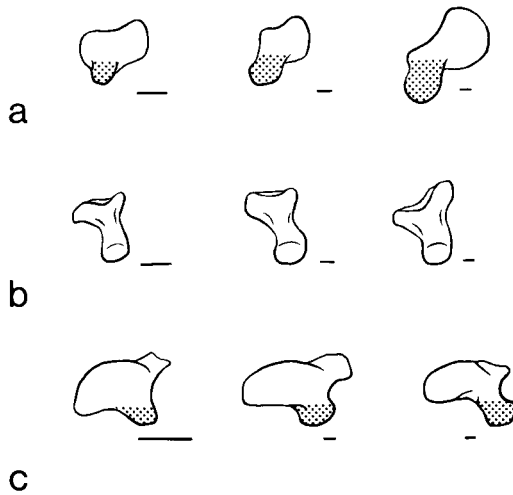


Fig. 3. Drawings of the (a) scaphoid, (b) pisiform, and (c) hamate in *Tupaia* (left), *Saimiri* (middle), and *Lemur* (right) showing the relatively elongate scaphoid tubercle (shaded), reduced pisiform body, and elongate hamate hamulus (shaded) of strepsirhines. Scale bars = 1 mm.

common body size ranges (Fig. 4a). This pattern is the exact opposite of that expected under the biomechanical model discussed earlier (Fig. 1), where the predominantly mesaxonic haplorhines were expected to have a relatively larger scaphoid tubercle than the primarily ectaxonic strepsirhines.

Bivariate plots also show that a morphocline exists between the two suborders in which strepsirhines have a relatively short pisiform body and haplorhines tend to have a somewhat taller pisiform (Fig. 3b). For example, monkeys and nonprimate eutherians such as *Tupaia* have a tall pisiform body, whereas that of *Lemur* is somewhat reduced (Fig. 3b). Bivariate plots (Fig. 4b) underscore this point and show that the two suborders differ significantly from one another in relative height of the pisiform body ( $P < .01$ ) (Tables 2, 3). A morphocline is apparent within the sample where monkeys, tarsiers, *Notharctus*, tree shrews, squirrels, and racoons all tend to share a relatively tall pisiform body, whereas strepsirhines appear derived in having a relatively reduced pisiform body (Fig. 4b). This pattern is again precisely the opposite of that expected under the biomechanical model

described earlier (Fig. 1), where the more ectaxonic strepsirhines were expected to have a tall pisiform body.

Finally, strepsirhine primates have a well-developed hamate hamulus compared to haplorhines and climbing nonprimate eutherians. The hamate hamulus, like the scaphoid tubercle, is relatively short in haplorhines compared to strepsirhines and is altogether absent in many tree shrews and squirrels (Fig. 3c). Bivariate plots again show that a morphocline exists between the two suborders in which monkeys, tarsiers, and *Notharctus* all have a relatively short hamate hamulus, whereas strepsirhines tend to have a well-developed hamulus (Fig. 4c). Bivariate tests show that strepsirhines differ significantly from haplorhines in relative length of the hamate hamulus ( $P < .01$ ) (Table 3), with strepsirhines having a relatively longer hamulus than haplorhines across common body size ranges (Fig. 4c).

The aforementioned osteometric results are summarized using a multivariate discriminant function analysis. The discriminant function classified 97% of the cases correctly and is highly significant ( $P < .001$ , Wilkes-Lambda). The discriminant axis shows a strong negative correlation with height of the pisiform body (Table 4), where the strepsirhines tend to have high scores on this axis and a relatively small pisiform body in contrast to the haplorhines, which have lower scores and a relatively larger pisiform body (Fig. 5). The only case which was classified incorrectly is *Daubentonia*, which groups with haplorhines in the discriminant analysis. *Daubentonia* has a tall, rod-like pisiform which contacts the radius, a condition unknown in other eutherian mammals (Nayak, 1933). The strong loading of pisiform height on the first discriminant axis explains why *Daubentonia* is classified with the haplorhines rather than the strepsirhines, since *Daubentonia*, like haplorhines, has a relatively expanded pisiform body (Nayak, 1933).

## DISCUSSION

The above morphometric analyses reveal that patterns of strepsirhine and haplorhine carpal morphology do not fit those expected

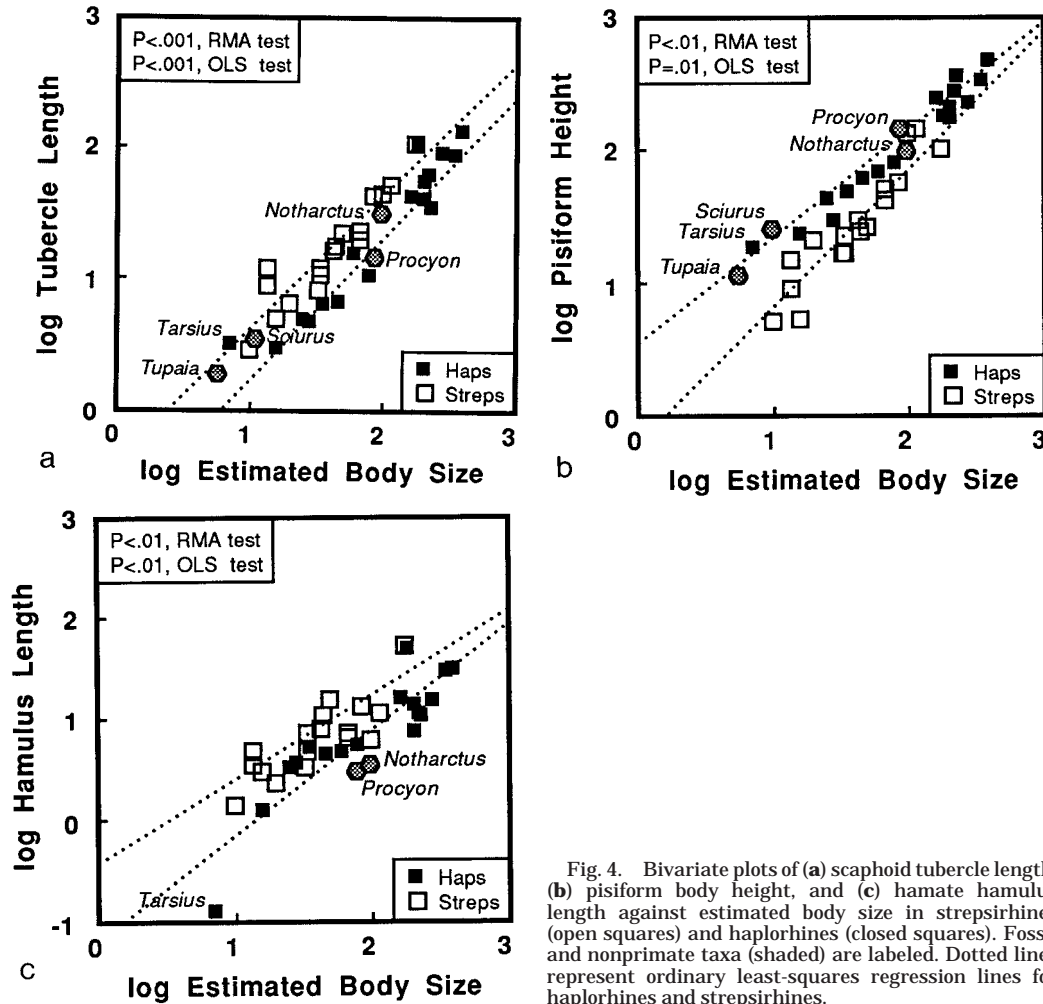


Fig. 4. Bivariate plots of (a) scaphoid tubercle length, (b) pisiform body height, and (c) hamate hamulus length against estimated body size in strepsirhines (open squares) and haplorhines (closed squares). Fossil and nonprimate taxa (shaded) are labeled. Dotted lines represent ordinary least-squares regression lines for haplorhines and strepsirhines.

TABLE 4. Canonical loadings and coefficients between carpal measurements and the first discriminant function axis of a MANOVA performed on log-transformed haplorhine and strepsirhine carpal dimensions<sup>1</sup>

Measurement	Canonical loading	Canonical coefficient
PISH	-.39	-3.82
RCW	-.20	.66
UCW	-.18	1.41
STL	-.07	1.84
HAL	-.01	-.32

<sup>1</sup> Measurement abbreviations are explained in the text.

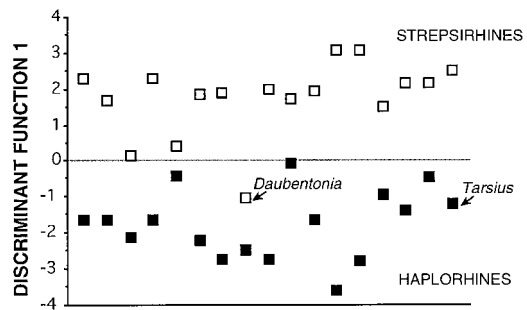


Fig. 5. Univariate plot of the first discriminant axis of a discriminant analysis performed on log-transformed linear carpal dimensions of strepsirhine (open squares) and haplorhine (closed squares) primates. The only case classified incorrectly is *Daubentonia*.

under Preuschoft et al.'s (1993) model. A recent study of primate hand postures (Schmitt and Lemelin, 1995) suggest that this is so because the kinematic assumptions upon which the biomechanical models are based are incorrect. Specifically, although ectaxonic primates do indeed use abducted hand postures on arboreal supports, the degree of abduction is often the same or less than that observed in arboreal mesaxonic primates (Schmitt and Lemelin, 1995; Lemelin and Schmitt, submitted). The hand postures and related muscle resultant forces (Fig. 1) attributed to haplorhines and strepsirhines by Preuschoft et al. (1993) therefore do not accurately reflect those of many arboreal mesaxonic and ectaxonic primates. Although both haplorhines and strepsirhines use ulnarly deviated hand postures, strepsirhines produce this movement primarily at the midcarpal joint, whereas haplorhines produce most of this movement at the metacarpophalangeal joints (Lemelin and Schmitt, submitted). The relatively large hamate and associated centrale-hamate contact of living strepsirhines (Beard et al., 1988) are then likely to be functionally related to frequent ulnar deviation at the midcarpal joint.

The underlying functional significance of the subordinal differences in carpal morphology presented here can be further understood by examining the soft tissue anatomy of the primate hand. The transverse carpal ligament, which forms the carpal tunnel, attaches primarily to the scaphoid tubercle and hamate hamulus, giving the ligament an oblique orientation (Fig. 6). Scaphoid tubercle length and hamate hamulus length are, not surprisingly, highly correlated ( $r = .89$ ,  $P < .001$ ) with one another in this sample. These bony structures are elongate in living strepsirhines, which deepens the carpal tunnel for well-developed tendons of the extrinsic digital flexors. The elongate scaphoid tubercle also serves as a windlass mechanism, which helps the pollical tendon of *m. flexor digitorum profundus* pull the thumb towards the palm in primates with a divergent, grasping pollex (Fig. 6). Relative pisiform size appears to have little influence upon carpal tunnel depth but is an important feature related to quadrupedal walk-

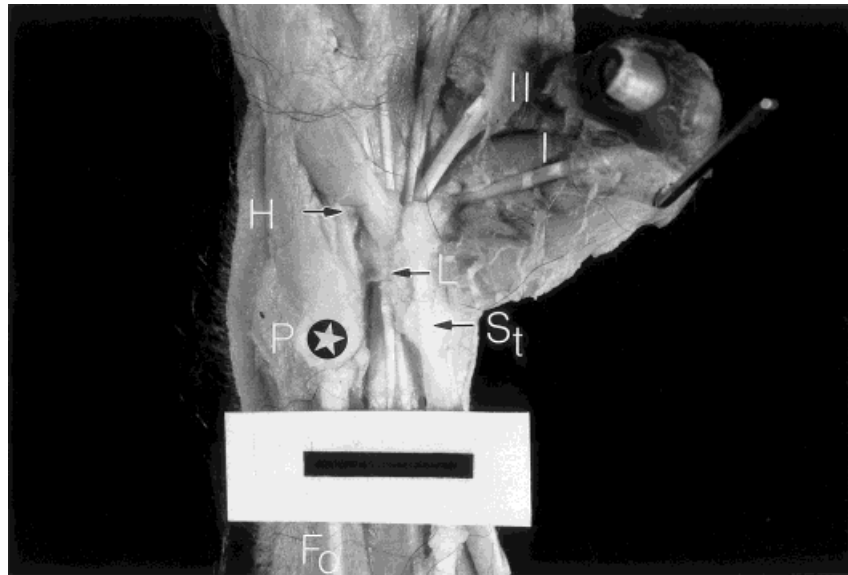
ing, running, and bounding. The elongate pisiform body of haplorhines increases the moment arm of *m. flexor carpi ulnaris* (FCU), a muscle which flexes the wrist from initially extended (= dorsiflexed) positions during the propulsive phase of quadrupedal locomotion (Whitehead, 1993), by placing its insertion further away from the joint center (Fig. 6) (Sarmiento, 1988; Hamrick, 1996b).

Haplorhines and adapiforms (including *Adapis* [Hamrick, 1996b]) share with nonprimate eutherians 1) a relatively tall pisiform body, which increases the moment arm for *m. flexor carpi ulnaris* (FCU), and 2) a relatively short hamate hamulus, indicative of a carpal tunnel that is relatively shallow compared to that of modern strepsirhines (Figs. 3, 4). Functionally, these bony features are related to 1) a flexor carpi ulnaris muscle that is afforded greater mechanical advantage to flex the wrist from extended positions compared to strepsirhines and 2) extrinsic digital flexors that are not so well developed as those of extant strepsirhines. Behaviorally, such features are associated with primarily quadrupedal locomotor behaviors. The presence of these features in adapiforms, tarsiers, monkeys, squirrels, raccoons, and tree shrews suggests that these are primitive mammalian features which were retained by the last common ancestor of Primates.

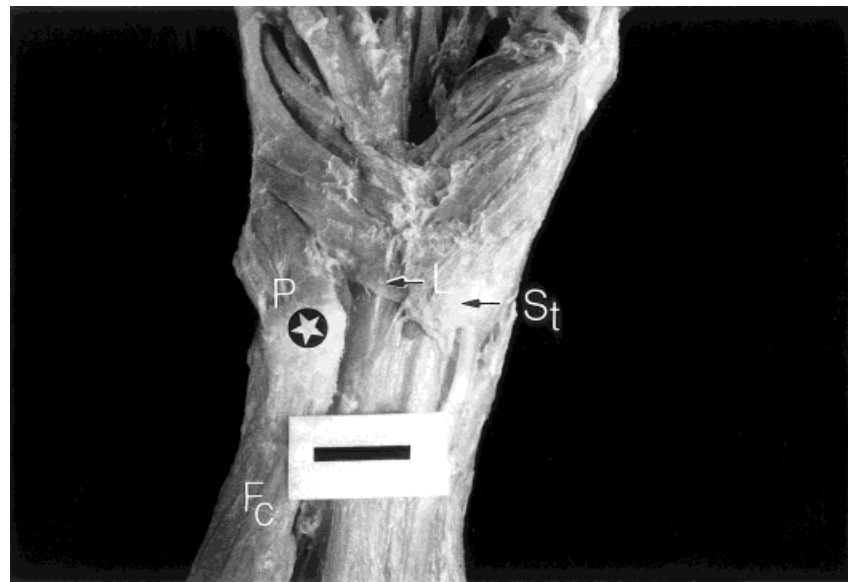
The taxonomic distribution of carpal characters referred to here indicates that an elongate scaphoid tubercle is shared by tarsiers, adapiforms, and strepsirhines but not tree shrews. Godinot and Beard (1991) considered a long scaphoid tubercle, large pisiform, and small hamulus to be primitive for primates, although they did not specify which of these features were derived for euprimates and which were not. Evidence

Fig. 6. Palmar views of the superficial hand musculature in *Otolemur* and *Papio* showing the obliquely directed proximal border of the transverse carpal ligament (L) which can be seen attaching primarily to the hamate hamulus (H) and scaphoid tubercle (S). The flexor carpi ulnaris muscle (Fc) inserts upon the palmar surface of the pisiform (P, Star). Note also that the pollical tendon of *m. flexor digitorum profundus* (I) is directed at a right angle relative to the long axis of the forearm in *Otolemur*, which has a very divergent pollex. The long flexor tendon to the second digit is also shown (II). Scale bars = 1 cm.





## *Otolemur*



## *Papio*

Fig. 6.

presented in this paper suggests that an elongate scaphoid tubercle is a derived feature of euprimates. A long scaphoid tubercle deepens the radial margin of the carpal tunnel and also acts as a windlass mechanism for the pollical branch of flexor digitorum profundus, which permits powerful thumb adduction from abducted positions. Altner (1971) also observed that primates differ from tree shrews in having a thumb complex that is relatively independent from the rest of the hand, and he too related this form-function complex to more effective manual grasping in primates. Behaviorally, structural adaptations for powerful pollical grasping are, like those adaptations for hallucial grasping, most likely related to clasping small-diameter arboreal substrates of irregular orientation (Cartmill, 1972, 1974).

The tendency for extant strepsirhines to possess both a relatively short pisiform body and an elongate hamate hamulus is not observed in the majority of primates (hominoids excepted) and climbing eutherians. Although there are certainly cases in which some strepsirhine species overlap with haplorhines in the relative expression of these traits and vice versa (e.g., Fig. 4b,c), there is nevertheless a clear indication that modern strepsirhines as a whole differ from other primate and eutherian groups in the development of these postcranial features. Hence, the relatively reduced pisiform and expanded hamulus of extant strepsirhines are likely derived features for primates and eutherians. The short pisiform body gives the flexor carpi ulnaris less power to flex the wrist from extended positions (Jouffroy, 1991; Hamrick, 1996b), indicative of a decreased commitment to quadrupedal locomotion and thus more frequent leaping and/or climbing behaviors (Dagosto, 1990; Hamrick, 1996b). The relatively short pisiform body of strepsirhine vertical clingers and even shorter pisiform body of strepsirhine slow climbers (Hamrick, 1996b) suggest further that pisiform reduction is correlated with a decreased commitment to palmigrade, quadrupedal locomotion. Pisiform reduction is especially obvious in humans, where the hand has been liberated entirely from its role as a locomotor organ (Jouffroy, 1991). The elongate hamulus increases the depth

of the carpal tunnel for well-developed extrinsic digital flexors, which are important for powerful manual grasping. As Napier (1961, p. 117) noted, "[T]he carpal arch is deepest in those forms in which finger flexion takes a dominant role in locomotion, and shallowest in those in which locomotion is of the more generalized quadrupedal type."

The morphoclines observed in osteometric analyses lend additional support to these functional interpretations. *Hylobates*, which has very powerful grasping hands and well-developed digital flexors (Tuttle, 1969, 1972), has the highest score of all the haplorhines in the discriminant function analysis (Fig. 5) and is therefore the most strepsirhine-like haplorhine in terms of its carpal tunnel morphology. *Daubentonia*, *Varecia*, and *Cheirogaleus*, which use horizontal supports frequently (Gebo, 1987; Oxnard et al., 1990; Dagosto, 1994), have the lowest scores of all the strepsirhines in the discriminant function analysis (Fig. 5) and are therefore the most haplorhine-like strepsirhines in terms of their carpal tunnel morphology. The powerful grasping hand of extant strepsirhines is well suited for the more frequent use of small-diameter supports and the use of these supports for clinging and climbing positional behaviors. This may also suggest a bias towards the use of vertical supports by the last common ancestor of tooth-combed prosimians (Gebo, 1986; Dagosto, 1988).

## CONCLUSIONS

Extant strepsirhine and haplorhine primates are quite similar to one another in the relative size of their radiocarpal and ulnocarpal articular surfaces. Extant strepsirhines (= lemuriforms) do, however, tend to differ from haplorhines, early Tertiary adapiforms, and nonprimate eutherians in having a reduced pisiform body and therefore a reduced lever arm for the flexor carpi ulnaris muscle. Lemuriforms also differ from these taxa in having a relatively well-developed hamate hamulus, whereas lemuriforms share with tarsiers and early Tertiary adapiforms a well-developed scaphoid tubercle. The elongate hamate hamulus and scaphoid tubercle of lemuriforms deepen the carpal tunnel for relatively large digital flexor tendons. The tendency for tooth-

combed strepsirhines to possess both a reduced pisiform and elongate hamulus appears to be derived relative to other primates and nonprimate arborealists. Results presented in this study show that lemuriform primates are distinguished from the majority of primates (including adapiforms) and nonprimate eutherians by several bony postcranial features that can be identified in fossils, in addition to their tooth comb. Moreover, results from this study indicate that the origin of tooth-combed primates was accompanied by a significant change in hand morphology, function, and substrate use.

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